

19 APR 1940
PRESENTED

ON *PHLYCTAENACHLAMYS LYSIOSQUILLINA*
GEN. AND SP. NOV., A LAMELLIBRANCH
COMMENSAL IN THE BURROWS OF
LYSIOSQUILLA MACULATA

BY
MARY LEYBORNE POPHAM, B.Sc.,
Department of Zoology, University of Bristol.

WITH TWENTY-ONE TEXT-FIGURES.

CONTENTS.

	PAGE
1. INTRODUCTION	62
2. HABITAT	62
3. EXTERNAL APPEARANCE AND HABITS	62
4. MANTLE AND SHELL	65
5. CTENIDIA	71
6. LABIAL PALPS	73
7. ALIMENTARY CANAL	73
8. FOOT	77
9. CIRCULATORY SYSTEM	77
10. EXCRETORY SYSTEM	77
11. NERVOUS SYSTEM	77
12. GENITAL SYSTEM	80
13. DESCRIPTION OF GENUS AND SPECIES	80
14. GENERIC AND SPECIFIC CHARACTERS	82
15. DISCUSSION	82
16. REFERENCES	83

1. INTRODUCTION.

A NUMBER of specimens of a commensal Lamellibranch with an internal shell and inhabiting the burrows of *Lysiosquilla maculata* were collected by Prof. C. M. Yonge during the course of the Great Barrier Reef Expedition. These differ in structure and habitat from any other Lamellibranch previously described, examination revealing that a new genus of the family Galeommatidae must be constituted to include this new species.

The specimens collected were preserved, some in Bouin's fluid, and others in 70% alcohol, and were handed over to the author for examination. One specimen was stained in borax carmine, and cleared in cedar-wood oil for examination of the entire animal. Serial transverse sections were prepared of another specimen and stained in Delafield's haematoxylin and eosin. Two other specimens were dissected under a binocular microscope.

Observations were made by Prof. C. M. Yonge on the habitat and appearance in life of this animal and his notes are incorporated in this paper, which has been prepared under his direction.

2. HABITAT.

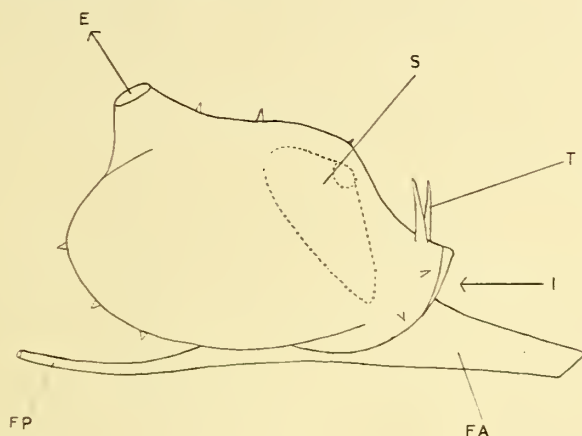
The tubes of *Lysiosquilla maculata*, one of the largest of the Stomatopoda, were common in the deep sand of the Sand Flat between the Sand Cay and the Thalamita Flat, as recorded by Stephenson, Stephenson, Tandy and Spender, in Vol. III, No. 2 of these Reports. The tubes were of great size with an internal diameter varying between 6.5 and 10 cm., and so extensive that an arm could be inserted up to the shoulder without the fingers coming in contact with the retreating occupant. The internal surface was very smooth. The external opening was much smaller, varying in diameter from 1 to 3 cm., but seldom being truly circular in outline. Fine sand from within the burrow was pushed over the edge to an extent of 4 to 5 cm., forming a ridged mound darker in colour than the surrounding surface sand. The overhanging ridge around the mouth of the burrows and the internal surface of these were very smooth, apparently owing to a viscid secretion produced by the occupant.

Within the tubes, usually near to the opening, were frequently to be found one, or occasionally two, small animals with white, fleshy bodies. Closer examination revealed that these were lamellibranchs with greatly reduced, internal shells. In some cases the animals moved about, in others they were secured by one or two fine byssus threads projecting from the posterior tip of the elongated foot.

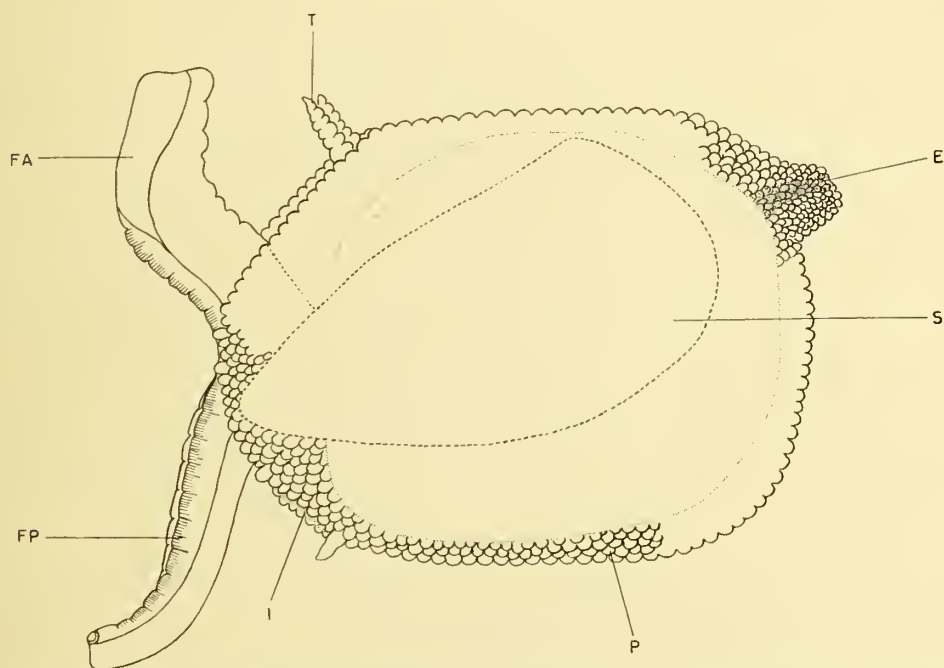
3. EXTERNAL APPEARANCE AND HABITS.

The appearance of the living animal is shown in Text-fig. 1, and the side view of a preserved specimen in Text-fig. 2. The body length of the largest specimen was, in life, 2.4 cm. The surface of the body is soft, white and partly translucent, and everywhere covered with small papillae which, when observed under a binocular microscope, have a slight brownish tinge. There are two conspicuous upward-directed tentacles (τ) at the anterior end of the dorsal surface. These are deep yellow, almost orange in colour except at the base, where they are white. A number of smaller tentacles, similar in colour, are scattered irregularly over the surface of the body, and are more numerous in larger

specimens. They appear to represent enlarged papillae. All have considerable powers of expansion and contraction, especially the large anterior pair, which give the animals, at first sight, the appearance of nudibranchs. The shell valves (s) are completely enclosed within the mantle, and are greatly reduced.



TEXT-FIG. 1.—View of the right side of the animal in life. $\times 2$. E, exhalent opening; FA, anterior portion of foot; FP, posterior portion of foot; I, inhalent opening; s, shell; T, tentacles.

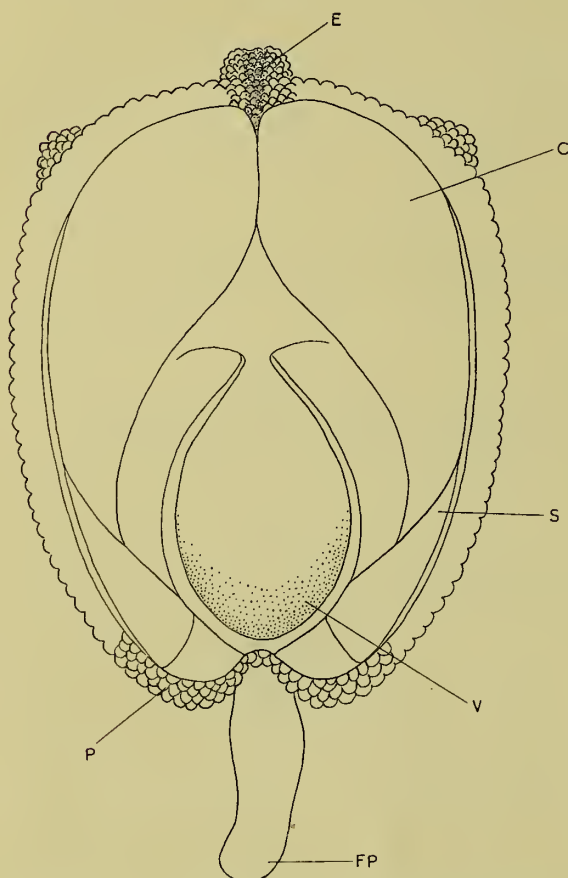


TEXT-FIG. 2.—Lateral view of the left side of a fixed specimen. $\times 12$. P, papillae. Other lettering as in Text-fig. 1.

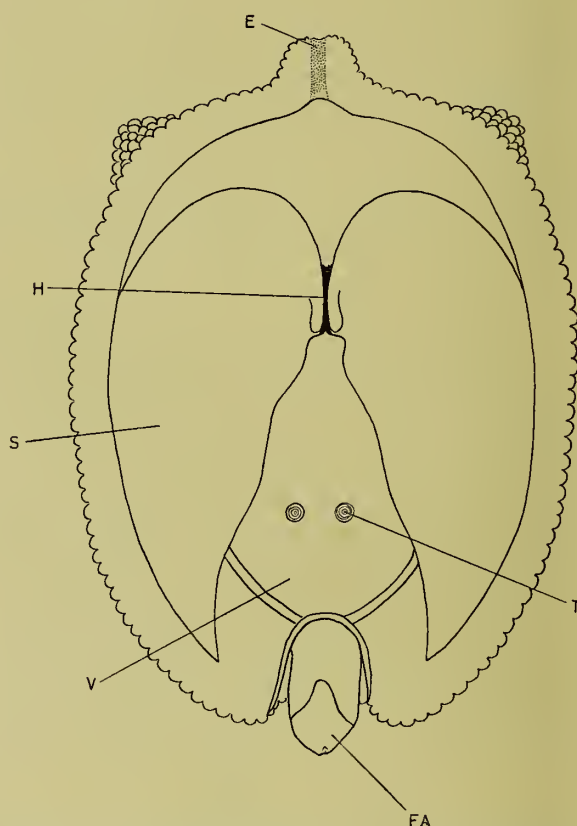
The inhalent opening (I) is anterior, and consists of that part of the antero-ventral pallial opening that is dorsal and anterior to the base of the foot. A prolongation of the mantle forms a "hood" over the anterior part of the foot, the edges of the mantle being here slightly turned back. The exhalent opening (E) is situated on the end of a conspicuous rounded protuberance in the mid-dorsal line near the posterior end. The lips of this open and draw in rhythmically when the animal is in motion, although the opening never

actually closes. The exhalent opening thus forms a more definite siphon than does the inhalent opening.

The pedal opening, which is continuous with the inhalent opening, extends from this backwards about one-third of the distance along the mid-ventral surface, the combined openings being sufficient to allow projection of the foot and the ingress of the food stream anterior and dorsal to this. The foot can be completely withdrawn, and the aperture



TEXT-FIG. 3.—Ventral view of a fixed specimen. $\times 12$. c, ctenidium; v, visceral mass. Other lettering as above.



TEXT-FIG. 4.—Dorsal view of a fixed specimen. $\times 12$. H, hinge. Other lettering as above.

closed by the apposition of the mantle edges. Posterior to the pedal opening the mantle edges are fused as far as the exhalent opening.

The foot is of considerable length when fully expanded, and consists of well-marked anterior (FA) and posterior (FP) regions. The anterior region is thicker, and is pushed out in a forward direction when the animal moves, resembling a long wedge about equal in length to the body. It possesses a creeping sole. The posterior portion is long and thin, with an opaque white area immediately short of the tip, which is sharply pointed. A byssus groove runs along the under surface and opens at the posterior end, from which byssus threads may project. Usually two of these were formed and planted between 30° and 90° apart when the animal was attached to the sides of the burrow. During movement the creeping sole advances and, at frequent intervals, the animal distends the mantle to the utmost extent and then, as a result of a convulsive movement which causes

a backward projection of water through the exhalent opening, the body is drawn forward, thereby overtaking to some extent the foot, which continues to advance slowly and without interruption. The posterior end of the foot, like a fine thread, trails behind and is capable of very great extension, up to 3 cm. in a specimen 2.4 cm. long.

In general external appearance the animal most nearly resembles *Chlamydoconcha orcutti* described by Bernard (1897). Both have a globular form, with a white, semi-transparent mantle covered with papillae, are about the same size, have a foot with a creeping sole, and the position of the inhalent and exhalent openings is similar. But *Chlamydoconcha* occurs in stony clam beds, and the shell is different.

4. MANTLE AND SHELL.

Histological examination of the mantle shows that beneath the epithelium it is composed of loose connective tissue, with very little structure (Text-figs. 12, M, and 20). It is thick, and the shell is completely embedded in it (Text-fig. 20). There are few blood-spaces, but a considerable amount of muscle.

A definite muscular layer occurs below the internal epithelium bounding the mantle cavity (Text-figs. 12–19, MS). The arrangement of the muscle-fibres is irregular, and both circular and longitudinal muscles are present. This muscle layer must be responsible for the repeated contractions of the mantle observed during movements of the living animal. The arrangement is such that contraction of the muscle would reduce the volume of the mantle cavity and force water out through the exhalent opening. Distension is presumably due to ciliary action drawing in water when the exhalent siphon is temporarily closed.

Fischer (1887) records similar convulsive movements, described as “sphincter-like contractions of the mantle”, in *Chlamydoconcha orcutti* which cause a current of water to pass over the gills.

The muscle forms a thick band towards the posterior end of the mantle cavity (Text-fig. 18, MS). There is also a well-marked muscular region round the anterior tips of the shell-valves (Text-figs. 12 and 13). The muscle layer is absent from the mantle on the dorsal side of the visceral mass in the centre of the animal (Text-figs. 14–17). Strands of muscle also occur in the outer layer of the mantle, just external to the shell (Text-fig. 12, MS), but the chief muscular region is in the inner mantle layer between the shell and the mantle cavity (Text-fig. 20, MS).

The mantle tissue between the shell and the mantle cavity is not so thick as that between the shell and the exterior. There is an irregularly-shaped cavity between the shell and the outer mantle layer (Text-figs. 13 and 20).

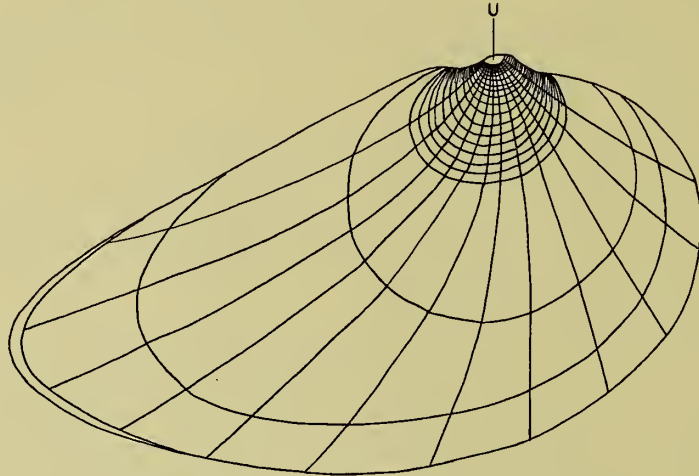
The papillae which cover the surface (Text-fig. 2, P) also contain connective tissue, together with many dark-staining goblet-cells which open externally (Text-fig. 12A, MU). These are typical mucous glands and occur in the papillae all over the body. They are particularly numerous in the “tentacles” or larger papillae. The papillae do not appear to have a sensory function: unlike the papillae in *Chlamydoconcha* (Bernard, 1897) they are not supplied by a nerve. Their function seems to be the secretion of mucus.

The “tentacles” are similar in structure to the papillae, but they are more specialized. They have longitudinal muscle strands in the centre and are capable of considerable contraction and expansion. Histologically the cells have a more granular appearance, in the contracted condition of the fixed material, than the cells of the small papillae.

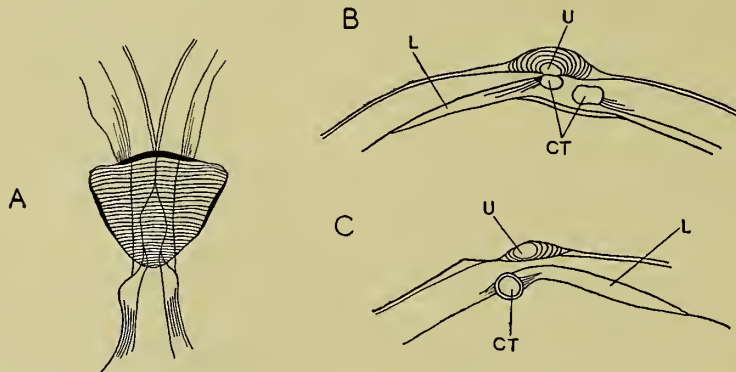
They contain more mucous glands, irregularly arranged (Text-figs. 1 and 13, τ). These small gland-cells also occur in *Chlamydoconcha* (Bernard, 1897), scattered over the surface of the mantle, but not on the papillae.

The internal surface of the mantle lining the mantle cavity is generally smooth, but there is irregular folding in parts (Text-fig. 18).

The shell measured 4.75 mm. \times 3.0 mm. in a specimen 6.0 mm. in body length. It is fragile and has little protective function, as it only covers a small part of the dorsal



TEXT-FIG. 5.—Shell. \times 12. u, umbo.



TEXT-FIG. 6.—A. Ligament. B. Right shell valve. C. Left shell valve. \times 25. ct, cardinal tooth; L, posterior lateral tooth.

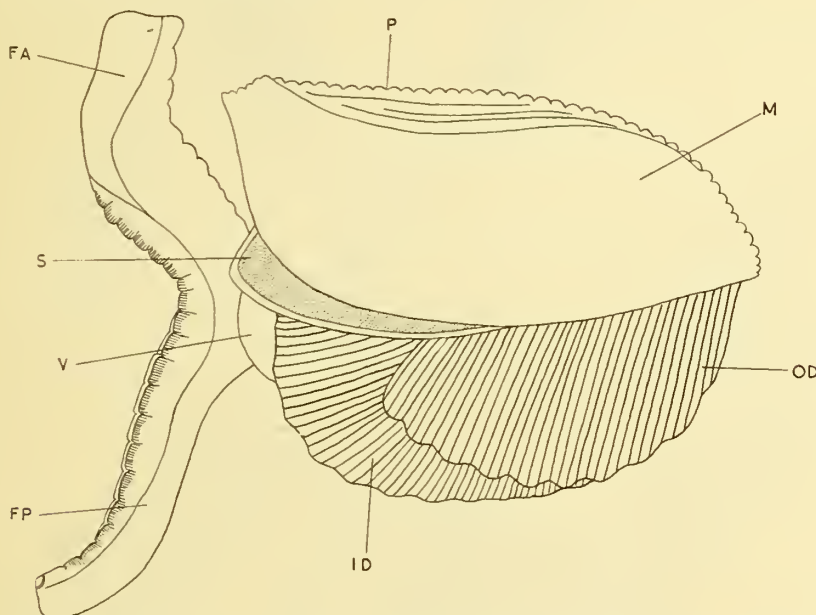
region of the visceral mass (Text-fig. 4, s). In shape it is equivalve, inequilateral, oval and flattened (Text-fig. 5). The valves are opposed only at the dorsal side in the region of the hinge. The ventral edges are always widely separated and can never be opposed, the visceral mass, ctenidia and foot, even in the contracted state, extending beyond them ventrally, anteriorly and posteriorly.

In colour the shell is pure white over most of the surface, but becomes yellowish towards the umbo. The surface is smooth, with fine lines radiating from the umbo, and also lines, presumably indicating previous growth stages, following the curve of the circumference of the shell. The edge of the shell is smooth and entire.

The umbo is situated one-third of the length from the posterior end; it is circular and convex and occupies the summit of the valve (Text-fig. 5, u). The posterior

end of the valve is short and rounded, while the anterior end is longer and more pointed, although the tip is blunt. The hinge-line is slightly curved. The hinge is situated in the region of the umbo below the summit of the valves. It is very poorly developed and the hinge teeth are small, blunt and rounded, with no means of interlocking. The hinge can, therefore, have little function.

On the left valve the cardinal tooth is represented by a round knob in the centre of the hinge, and slightly anterior to the summit of the umbo (Text-fig. 6C, CT). On the right valve the cardinal tooth is probably represented by two knobs; one immediately below the summit of the umbo is rounded and prominent, the other is anterior to the umbo and is broader and less prominent (Text-fig. 6B, CT). There are no anterior lateral teeth. The posterior lateral teeth are reduced to a ridge on the left valve, and to a socket between two ridges on the right valve (Text-fig. 6C, L).



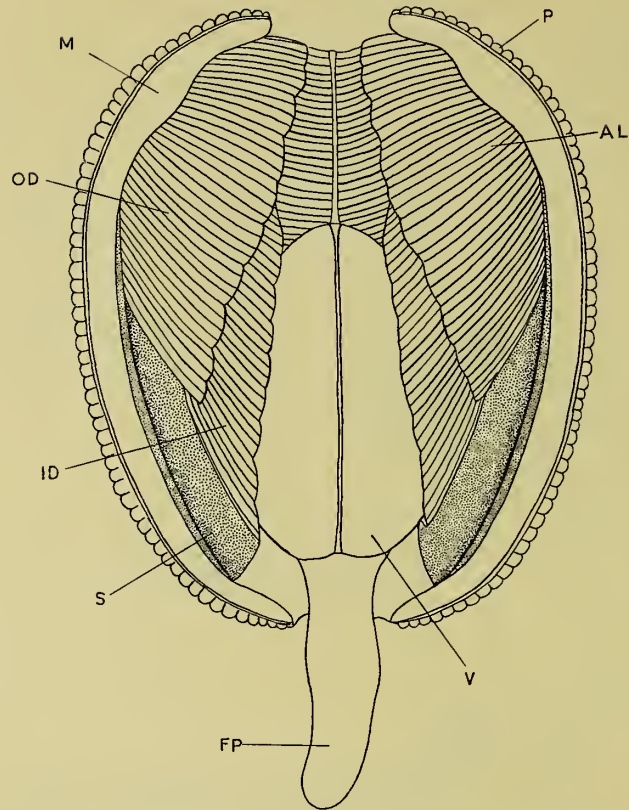
TEXT-FIG. 7.—Lateral view of the left side of a fixed specimen with the mantle turned back. $\times 12$.
ID, inner demibranch; M, mantle; OD, outer demibranch; other lettering as above.

The shell valves are held together by an internal elastic ligament, inserted below the umbo. It is thick, dark brown in colour, and triangular in shape, with the base of the triangle situated posteriorly (Text-fig. 6A).

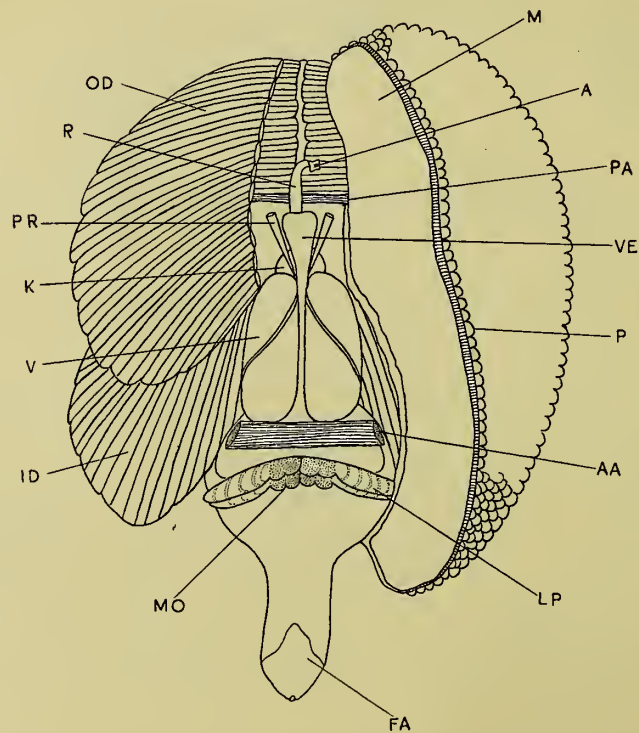
The periostracum is well marked on the outer surface of the shell, and is also visible on the inner side at the edge of the shell (Text-fig. 20, PO).

The adductor muscles are poorly developed, and leave no impressions on the inner surface of the shell valves. Little movement of the shell valves occurs in life. The anterior adductor muscle is larger than the posterior, and is situated on the dorsal surface of the visceral mass over the oesophagus. It lies behind the labial palps and immediately above the cerebro-pleural ganglia (Text-fig. 9, AA). The posterior adductor muscle is small; it is situated at the posterior end of the visceral mass below the rectum and behind the heart (Text-fig. 9, PA).

The morphological relationships of the shell and mantle call for comment. In the Lamellibranchia the free margin of the mantle normally consists of three folds (Text-fig.

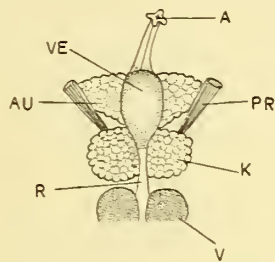


TEXT-FIG. 8.—Ventral view with the mantle removed. $\times 12$. AL, ascending lamella. Other lettering as above.

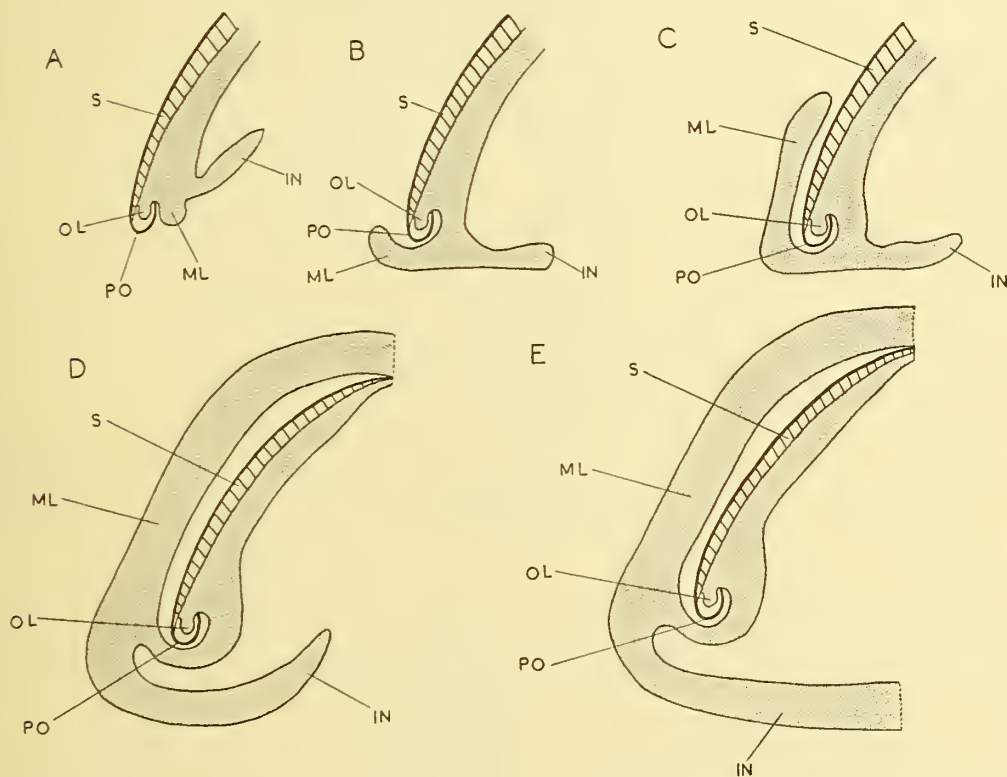


TEXT-FIG. 9.—Dorsal view with the mantle removed. $\times 12$. A, anus; AA, anterior adductor; K, kidney; LP, labial palps; MO, mouth; PA, posterior adductor; PR, pedal retractor; R, rectum; VE, ventricle. Other lettering as above.

11A). The outer fold is always secretory in function; the middle fold is usually sensory, and the inner fold forms the velum or pallial curtain where one is present (Yonge, 1936). In the animal here considered each valve is enclosed in the mantle, being completely surrounded by it. As described below, this condition has probably arisen owing to an overgrowth of the shell by the middle fold of the mantle.



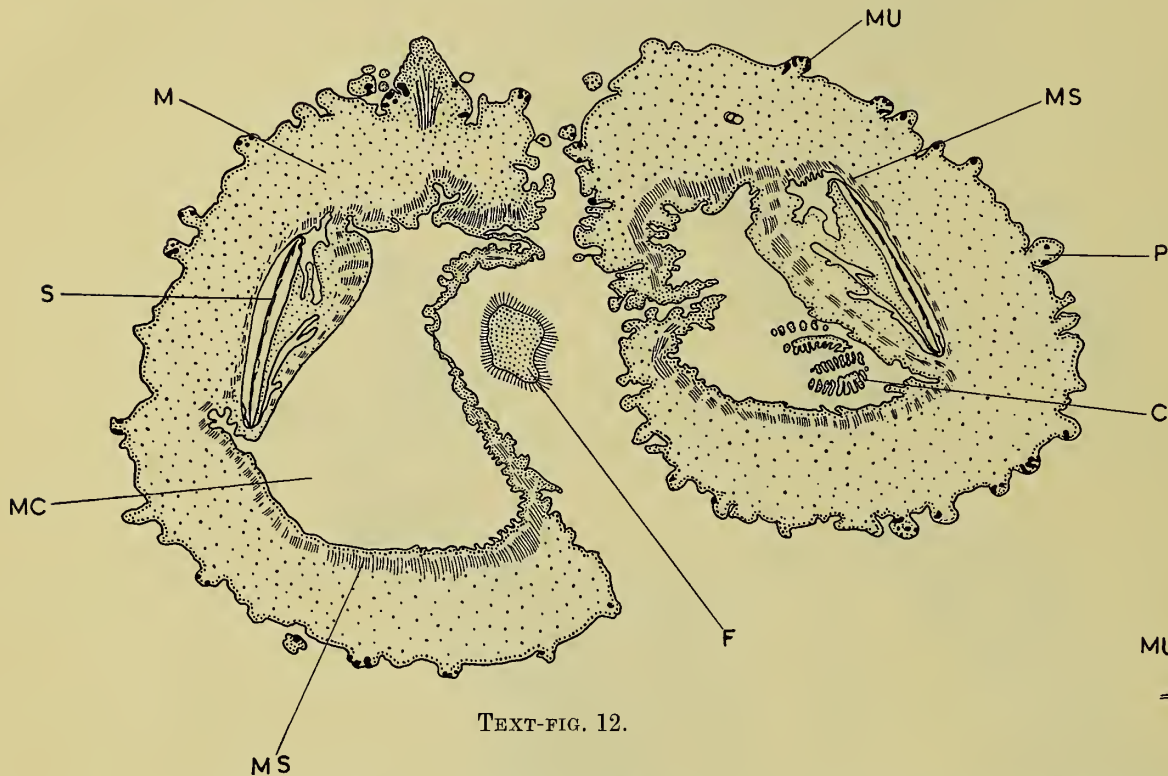
TEXT-FIG. 10.—Heart region. $\times 25$. AU, auricle. Other lettering as above.



TEXT-FIG. 11.—Relation of the mantle to the shell. A. Normal Lamellibranch. B. Hypothetical stage. C. Condition in *Scintilla*. D and E. Condition in *Phlyctenachlamys lysiosquillina*. IN, inner mantle lobe; ML, middle mantle lobe; OL, outer mantle lobe; PO, periostracum; S, shell.

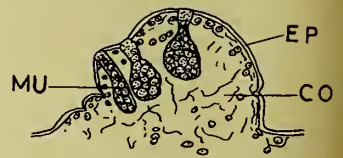
The outer fold of the mantle remains secretory in function and produces the shell. This fold remains in the normal position immediately internal to the margins of the shell (Text-fig. 11, OL). The irregular cavity between the shell and this outer mantle fold is only present in some places, and is probably an artifact due to fixation. The periostracum, as in other Lamellibranchia, is formed at the base of the groove on its inner side, and extends over the edge of the shell as shown in Text-fig. 11, PO.

Differential growth of the middle fold of the mantle has probably taken place, first in a ventral direction and then dorsally over the outer surface of the shell (Text-fig. 11, ML). A hypothetical early stage of this overgrowth is shown in Text-fig. 11B. A further stage is found in *Galeomma* in which the mantle is reflected for a short distance over the anterior, posterior and ventral borders of the shell. In *Scintilla*, as shown in Text-fig. 11C, more of the shell is covered by the mantle (Deshayes, 1855). The final stage is shown in Text-figs. 11 D and E, and represents the condition found in this specimen. The overgrowth is complete, and the middle mantle fold fuses in the mid-dorsal line with the middle fold of the opposite side. It also extends anteriorly and posteriorly. The fusion is complete posteriorly and dorsally except for the exhalent aperture. Anteriorly the



TEXT-FIG. 12.

TEXT-FIG. 12.—Transverse section through the anterior end. $\times 33$. F, foot; MC, mantle cavity; MS, muscle layer; MU, mucous gland cell. Other lettering as above. TEXT-FIG. 12a.—Papilla enlarged. $\times 200$. co, connective tissue; EP, epithelium.



TEXT-FIG 12a.

mantle folds form the sides of the inhalent siphon. The line of fusion cannot be detected in histological examination.

The presence of a groove between the inner and middle mantle lobes on the inner side of the ventral extremity of the shell, and the irregular cavity between the shell and the mantle lying over it, support this interpretation. It also supplies an explanation for the presence of "tentacles", as the middle fold normally bears sense-organs, although the sensory function appears to be lost in this case.

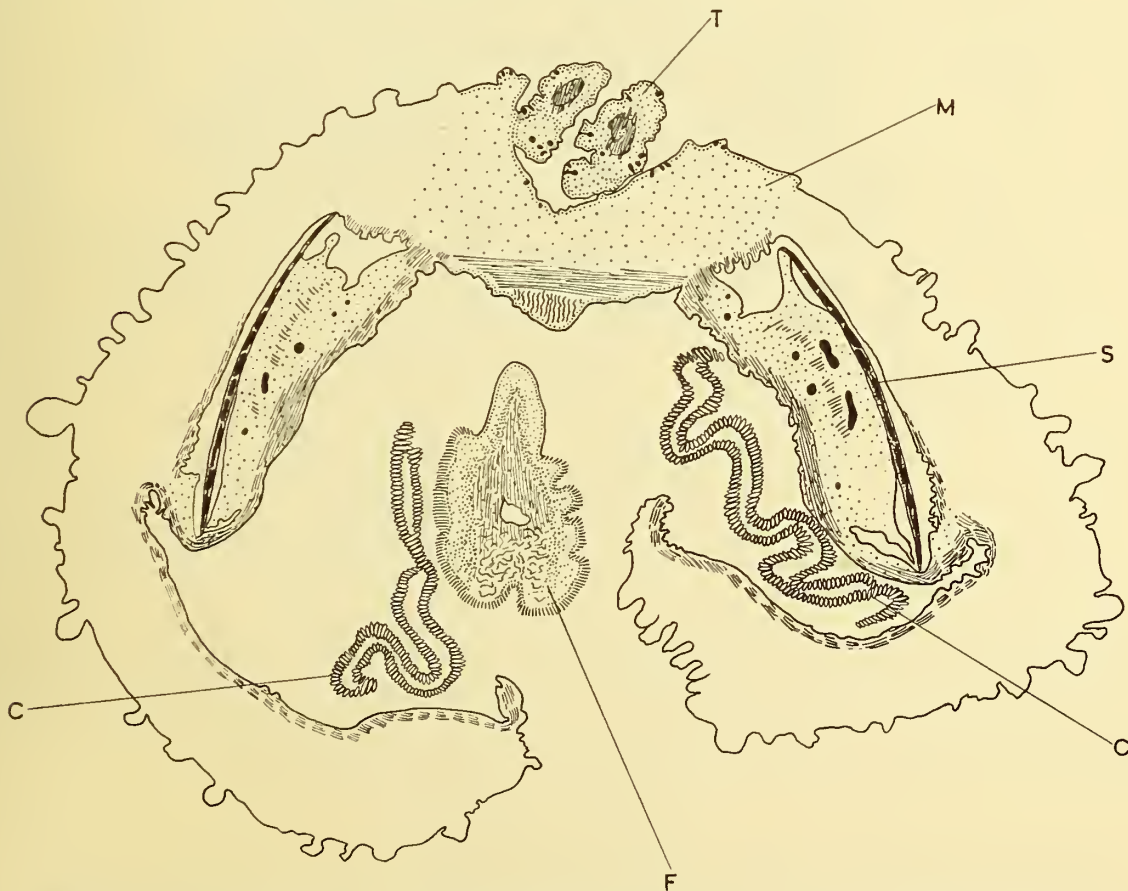
The inner mantle fold forms the velum or pallial curtain in genera such as *Pecten* or *Ostrea* where the mantle edges are not fused ventrally. This is highly muscular, and performs extensive movements primarily concerned with controlling the entrance of water into the mantle cavity, *e. g.* in *Ostrea*, but modified in connection with swimming

in *Pecten*. Where fusion of the mantle lobes takes place, it is the inner mantle folds which fuse, and in the present case it is suggested that the inner fold grows inwards and fuses with the inner fold from the opposite side in the mid-ventral line, behind the pedal opening (Text-fig. 11, IX). There is again no histological evidence of this fusion, but the chief muscular region occurs in this part of the mantle, beneath the epithelium bounding the mantle cavity (Text-fig. 12, MS), and similar fusion of the mantle is found in very many Enlamellibranchia.

5. CTENIDIA.

The ctenidia each consist of two demibranchs formed of a descending or direct lamella and an ascending or reflected lamella. The ctenidia are inserted dorsally behind the main part of the visceral mass. The axes are supported by the lesser reno-pericardial mass, the ascending lamellae of the outer demibranchs by the mantle, and the ascending lamellae of the inner demibranchs join in the mid-line below the reno-pericardial mass (Text-figs. 9 and 13). The inner demibranch extends farther forwards and downwards and has a more pointed anterior tip than the outer demibranch (Text-fig. 7, ID).

In fixed material the ctenidia appear to be plicated, the plicae occurring at regular intervals (Text-figs. 7-9). Histological examination shows, however, that there are no principal filaments, so the apparent plication may be due to fixation.



TEXT-FIG. 13.—Transverse section through the tip of the foot. $\times 33$. Lettering as above.

The structure of the ctenidia is very simple. The filaments are regular in arrangement with interfilamentary junctions formed by horizontal bars (Text-fig. 21, J). The lamellae of each demibranch are widely separated, with *no* interlamellar junctions. This unusual condition may be correlated with the distension and contraction of the mantle during life, and with the reduction of the shell and adductor muscles. In the fully distended condition the valves must be raised until they become almost horizontal in position, at the same time pulling out the ctenidia so that the lamellae of each demibranch are separated. This could not occur if they were connected by interlamellar junctions. When water has been



TEXT-FIG. 14.—Transverse section through the mouth. $\times 33$. AP, anterior pallial nerve; BG, byssal gland; IP, inner labial palp; OP, outer labial palp; PN, pedal nerve; v, anterior end of the visceral mass. Other lettering as above.

expelled through the exhalent siphon the volume of the mantle cavity is reduced, the valves lowered, and the ctenidia returned to their normal position with the two lamellae of each demibranch lying close together. According to Ridewood (1903), interlamellar junctions are present in all other members of the family Galeommatidae.

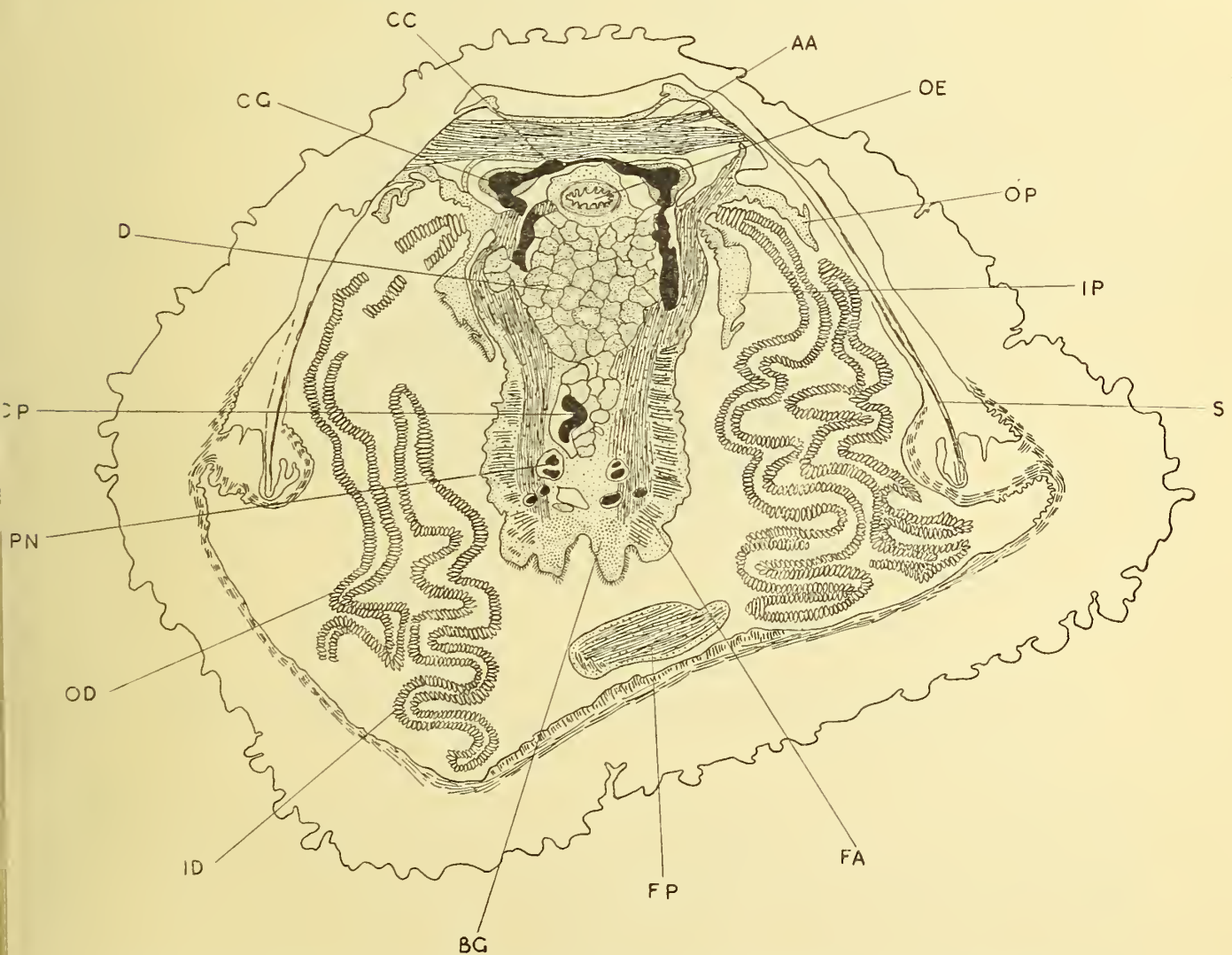
6. LABIAL PALPS.

The two pairs of labial palps have the form of smooth flat blades with rounded tips (Text-fig. 9, LP), which extend laterally on either side of the mouth and curve down slightly

into the mantle cavity on either side of the anterior tip of the inner demibranch (Text-fig. 14, IP, OP). The free portion of the upper palp extends, therefore, to a position between the termination of the two demibranchs. The anterior median portions of the palps form the lips of the mouth, fusing in the mid-line and forming a solid oval band round the mouth. The opposed surfaces of the free portions of the palps are ridged, with a ciliated epithelium and many mucous glands. Cilia were not visible in fixed material on the outer surface of both pairs of palps, but they are probably present in life.

7. ALIMENTARY CANAL.

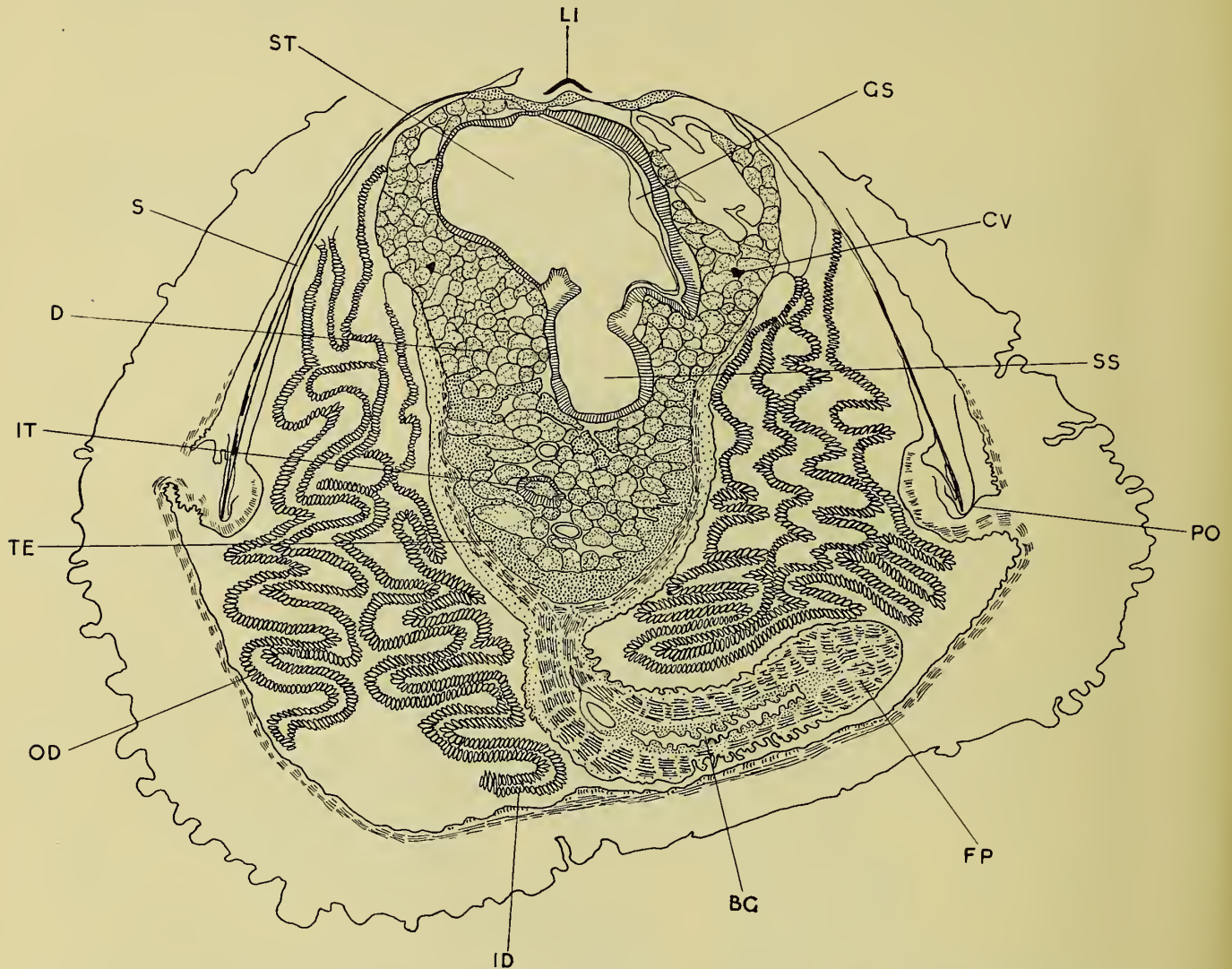
The mouth is at the anterior end of the visceral mass, opposite the inhalent opening. It opens between the two lips formed by the median portion of the labial palps, being hidden by the upper pair (Text-fig. 14). The surface of the mouth is folded and the



TEXT-FIG. 15.—Transverse section through the cerebro-pleural ganglia. $\times 33$. cc, cerebro-pleural commissure; CG, cerebro-pleural ganglia; CP, cerebral peduncle; D, digestive diverticula; OE, oesophagus. Other lettering as above.

ciliated epithelium contains many mucous cells. The lower lip is fused with the visceral mass.

The mouth opens into the oesophagus, which is centrally situated below the anterior adductor muscle. It is oval in cross-section and similar in structure to the mouth, the epithelium being surrounded by a narrow band of circular muscle (Text-fig. 15, oE). It

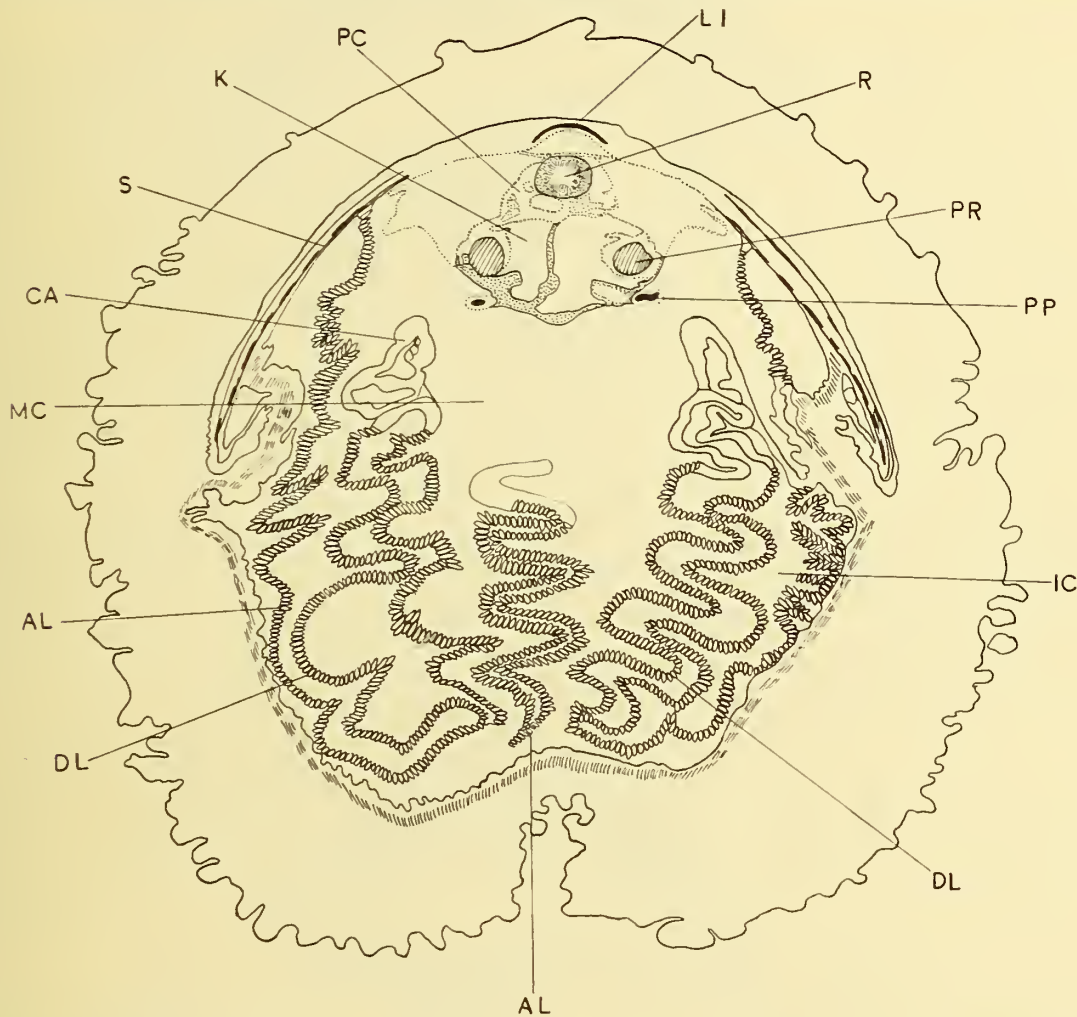


TEXT-FIG. 16.—Transverse section through the stomach. $\times 33$. cv, cerebro-visceral commissure; gs, gastric shield; it, intestine; li, ligament; ss, style-sac; st, stomach; te, testis. Other lettering as above.

passes direct to the stomach, which is slightly more ventral in position and is surrounded by the digestive diverticula. This wide, oval cavity occupies a large part of the visceral mass; it is lined with ciliated epithelium and has many mucous cells (Text-fig. 16, st). At the posterior end the stomach loses its oval shape and becomes irregular in outline.

A large style-sac opens into the stomach to the right of the mid-ventral line. It extends ventrally into the mass of digestive diverticula (Text-fig. 16, ss), and is separate from the intestine. A smooth gastric shield covers the wall of the stomach opposite the opening of the style-sac (Text-fig. 16, gs).

The digestive diverticula occupy most of the visceral mass, surrounding the alimentary canal from mouth to rectum (Text-fig. 15, D). In structure they consist of a mass of ramifying tubes, oval or round in cross-section, and clearly separated from each other. These tubules are lined with cubical cells containing granules, they open into ducts lined with flat ciliated epithelium, which unite and open through the ventral and lateral walls of the stomach, anterior to the style-sac. There are many separate openings, as noted by



TEXT-FIG. 17.—Transverse section through the rectum and the kidney. $\times 33$. AL, ascending lamella; CA, axis of the ctenidium; DL, descending lamella; IC, interlamellar cavity; PC, pericardium; PP, posterior pallial nerve. Other lettering as above.

Bernard (1897) in *Chlamydoconcha*, but they form three main groups, one ventral, and two lateral.

The intestine leaves the stomach just anterior to the opening of the style-sac, and to the right of the mid-ventral line. It coils about through the mass of digestive diverticula, remaining ventral to the stomach throughout its course (Text-fig. 16, IT), except during the last coil, when it passes forwards and upwards to the right of the stomach. Behind the stomach the intestine passes upwards in a loop through the posterior end of the gonad, on a level with the middle of the stomach. It gradually becomes more dorsal, finally merging into the rectum. The intestine has no typhlosole.



TEXT-FIG. 18.—Transverse section through the posterior adductor. $\times 33$. Lettering as above.



TEXT-FIG. 19.—Transverse section through the anal region. $\times 33$. Lettering as above.

The rectum is a straight circular tube. It has no mucous glands; this is possibly correlated with the powerful expulsion of water through the exhalent siphon rendering the elaboration of firm faecal pellets unnecessary. The rectum passes through the ventricle of the heart, over the posterior adductor (Text-figs. 17 and 18, R), and opens by a dorsally directed anus into the mantle cavity, below the exhalent siphon (Text-fig. 19, A).

The whole of the alimentary canal, with the exception of the region bearing the gastric shield, is strongly ciliated.

8. FOOT.

Histologically the foot is a compact mass of muscle with many blood spaces in the centre. It is also well supplied with nerves (Text-figs. 12-16, FA, FP). The ventral surface of the foot, together with the sides of the byssal groove, is ciliated. These cilia are probably responsible for the slow gliding motion of the foot in life.

In the anterior portion of the foot there are typical mucous glands, the mucus produced lubricating the creeping sole of the foot. They are most numerous ventrally, but they also extend up the sides of the foot at the anterior tip; farther back they are confined to the ventral side, and eventually mingle with the byssal gland-cells.

The byssal gland consists of dark-staining cells concentrated round the inner portion of the byssal groove, but extending for a considerable depth into the pedal mass. The gland is dense in the central portion of the foot, and extends above the byssal groove throughout the posterior portion of the foot, except for the extreme posterior tip.

The paired pedal retractor muscles are inserted into the posterior portion of the shell, just anterior to the anus, and immediately above the posterior adductor muscle (Text-figs. 9 and 18, PR). They are most widely separated at the posterior end. They pass forwards on either side of the heart and kidneys (Text-fig. 17, PR), to either side of, and above the visceral ganglia. The two muscles join below the intestine, and pass into the substance of the visceral mass at its posterior end. They pass down either side of the posterior part of the gonad, and into the muscular mass of the foot.

The pair of pedal protractor muscles are slender. They pass forwards on either side of the oesophagus, remaining below the anterior adductor muscle and the cerebro-pleural commissure, and enter the anterior portion of the foot in front of the cerebro-pleural ganglia.

9. CIRCULATORY SYSTEM.

The pericardial cavity is posterior and dorsal to the visceral mass. It is situated between the two pedal retractor muscles, in the mid-line immediately behind the kidneys (Text-fig. 17, PC). It contains the heart, which consists of a ventricle and two lateral, thin-walled auricles (Text-fig. 10, AU).

The blood-vessels are not well defined, except near the heart, where anterior and posterior vessels leave the heart in the mid-line. Two lateral vessels enter the auricles close to the mid-line, they come from the visceral mass.

10. EXCRETORY SYSTEM.

The kidneys are small. They are situated just anterior to the heart and, with the pericardium, form a distinct mass separate from the main portion of the visceral mass, and posterior and dorsal to it (Text-fig. 10, K). At the anterior end there are two distinct

organs, one on either side of the rectum and separated by the anterior end of the pericardium. As the pericardium narrows posteriorly, the two kidneys enlarge towards the mid-line. They end posteriorly in a point beneath the posterior adductor muscle. Anteriorly they extend as far as the posterior end of the gonad. A ciliated duct from each kidney opens into the pericardium immediately above the pedal retractor muscle, on either side of the rectum, and below the posterior end of the gonad. The opening from the kidneys into the mantle cavity has not been observed.

The pericardial gland is situated on the lateral walls of the pericardium, and also covers the lateral walls of the anterior end of the ventricle. It extends, at the level of the axes of the ctenidia, throughout the greater part of the pericardium, and ends above the posterior face of the visceral ganglia, and opposite the auricles. It consists of a dense mass of cells which contain granules and have large nuclei.

11. NERVOUS SYSTEM.

The nervous system is normal and the ganglia are large. The cerebro-pleural ganglia are situated behind the mouth, on either side of and slightly above the oesophagus (Text-fig. 15, CG), they are joined by a large cerebral commissure, which passes over the oesophagus and under the anterior adductor muscle (Text-fig. 15, CC).

Large pallial nerves leave the anterior face of the cerebro-pleural ganglia, and pass forwards on either side of the mouth, becoming slightly more dorsal in position and farther apart (Text-fig. 14, AP). They lie in the mantle, close under the shell, and become farther apart as the anterior tips of the shell valves separate. Towards the tip of the shell the pallial nerves divide up into many small nerves, which spread out in the tissue of the mantle inside the shell. The main branch of the nerve is situated centrally beneath the shell. At the extreme anterior end the small nerves lie just below the muscle layer that borders the mantle cavity.

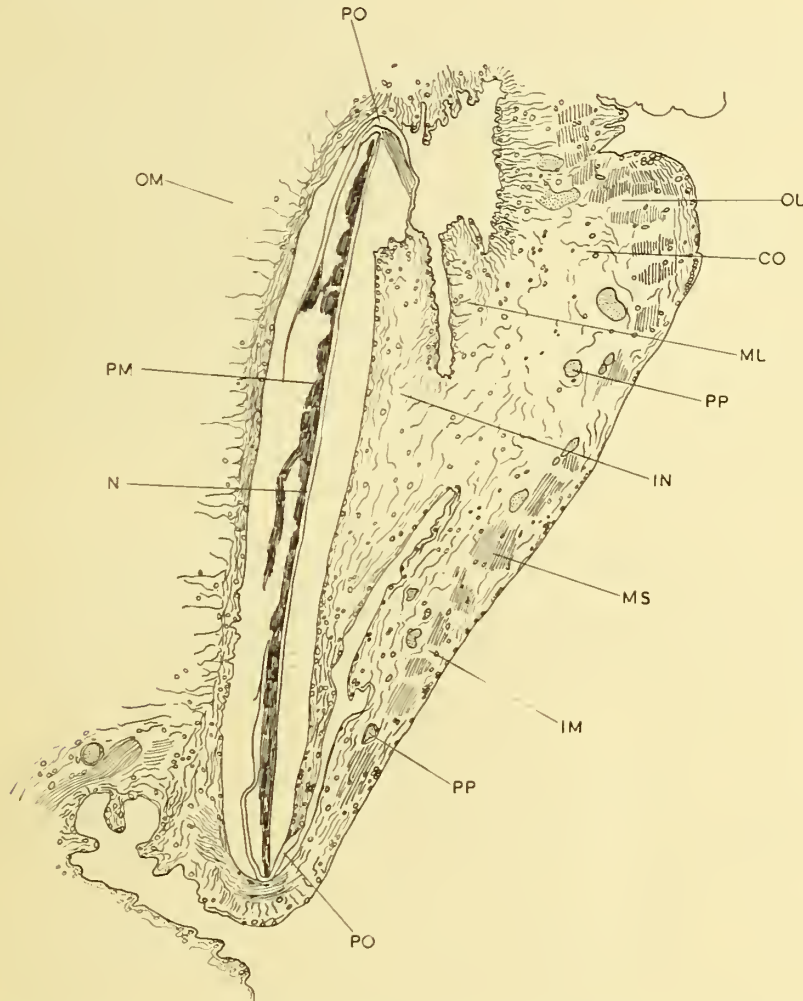
The cerebro-pedal commissures leave the posterior ventral face of the cerebro-pleural ganglia, and pass vertically downwards into the foot between the mass of digestive diverticula and the wall of muscular tissue that bounds them (Text-fig. 15, CP). Upon reaching the muscular mass of the foot the nerves pass backwards in the centre of the foot on either side of the median line and into the pedal ganglia at their anterior face.

The pedal ganglia are situated in the central portion of the foot at the approximate dividing line between the anterior and posterior portions. They lie between the byssal gland at the ventral side of the foot and the gonad. The ganglia are large and joined together in the mid-line.

Large pedal nerves pass forwards from the ganglia on either side of the mid-line into the anterior portion of the foot, and divide up into many smaller nerves. The whole of the anterior portion of the foot is richly innervated (Text-fig. 15, PN). Posterior pedal nerves leave the posterior face of the pedal ganglia. They are smaller than the anterior pedal nerves and supply the posterior portion of the foot. Like the anterior pedal nerves, they divide up into many small nerves.

The cerebro-visceral commissures leave the posterior face of the cerebro-pleural ganglia; they pass back on either side of the oesophagus, becoming farther apart and more ventral in position. They are smaller than the cerebro-pedal commissures or the anterior pallial nerves. They pass between the mass of digestive diverticula, and the muscular

wall of the visceral mass, and are at the same level as the axes of the ctenidia (Text-fig. 16, cv). They lie close to the wall of the stomach at its posterior end, approach the median line behind it and then extend beneath the dorsal portion of the gonad. They continue on either side of the heart, above and outside the pedal retractor muscles, and pass towards the mid-line beneath the posterior end of the heart. They enter the visceral ganglia at their anterior face beneath the rectum.



TEXT-FIG. 20.—Transverse section through the mantle and the shell. $\times 75$. IM, inner layer of the mantle; N, nacreous layer of the shell; OM, outer layer of the mantle; PM, prismatic layer of the shell. Other lettering as above.

The visceral ganglia are the largest of the ganglia and are situated behind the main visceral mass, beneath the pericardium and excretory organs. They lie close together, and are joined in the mid-line into one large ganglionic structure.

A large branchial nerve passes from the external lateral side of each visceral ganglion into the main axis of one of the ctenidia, continuing along this and sending branches into the descending lamellae of each demibranch. A nerve passes from the ventral face of each ganglion into the ascending lamellae and along the axes, sending branches into each lamella. A nerve also leaves the posterior face of each ganglion. These two nerves separate and pass beneath the pedal retractor muscles and the pericardium. Posteriorly

they become farther apart and pass into the tissue of the mantle inside the shell, where they divide up into many small nerves. They remain below the posterior adductor muscle. There are three main branches which lie close under it, one in the mid-line, and two laterally (Text-fig. 18, PP). The whole of the mantle inside the shell is richly innervated (Text-fig. 20, PP).

12. GENITAL SYSTEM.

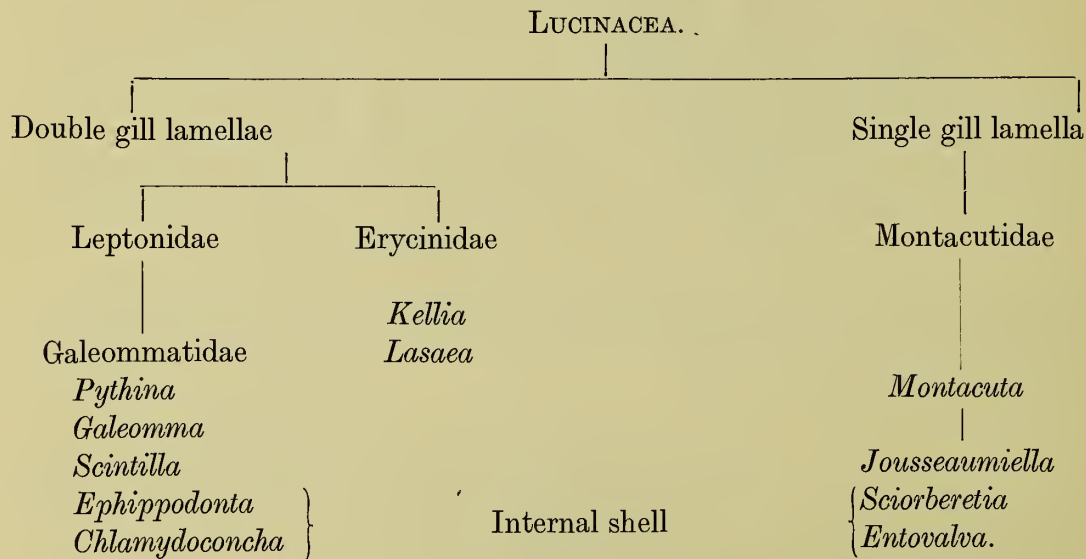
The specimen sectioned was a male, and the testis, composed of ramifying tubules, contained sperms in all stages of development.

The testis extends forwards above the foot, to the level of the pedal ganglia. At the anterior end it is confined to the ventral side of the visceral mass, and is spread out over the ventral surface of the digestive diverticula (Text-fig. 16, TE). The mass of the gonad is small compared with that of the digestive diverticula. Behind the style-sac the testis spreads out dorsally and composes most of the posterior part of the visceral mass. It surrounds the hinder, part of the intestine. At the posterior end of the visceral mass the testis becomes more dorsal in position, and forms a compact mass surrounding the rectum.

The testis opens by a short ciliated funnel into the mantle cavity on either side. The opening leads into the supra-branchial cavity in the region above the inner demibranch, immediately over the cerebro-visceral commissure, and just anterior to the opening of the excretory organ into the pericardium.

13. DESCRIPTION OF GENUS AND SPECIES.

According to Pelseneer's classification (Pelseneer, 1911), the Order Lucinacea is divided into two groups according to whether the ctenidia have one or two demibranchs:



The Erycinidae are distinguished by the presence of three pallial openings, whereas the members of the other three families have two. The Erycinidae and Montacutidae are hermaphrodite, with incubation of the embryos in the mantle cavity. In the Leptonidae and Galeommatidae the sexes are separate, and the mantle has papillae. The distinction between the two families lies in the position of the shell in relation to the mantle. In the

Leptonidae the shell is always external, but in the Galeommatidae the mantle covers the shell to a varying degree. In *Pythina* (Pelseneer, 1911) the mantle is only reflected over the extreme edge of the shell. In *Galeomma* and *Scintilla* (Fischer, 1887) the mantle is reflected for some distance over the edges of the shell valves, while in *Ephippodonta* (Tate, 1887) and *Chlamydoconcha* (Bernard, 1897) this reflection of the mantle has advanced to such an extent that the shell is completely internal. In the Erycinidae the shell is always external, but a similar development to that in the Galeommatidae has taken place in the Montacutidae. *Montacuta* has an external shell with no reflection of the mantle lobes. *Jousseaumiella* (Bourne, 1906) also has an external shell, but in *Sciorberetia* (Bernard, 1895) and *Entovalva* (Ohshima, 1930) the shell is completely enclosed in the mantle as it is in *Ephippodonta* and *Chlamydoconcha*.

Modification in the position of the shell valves has also occurred in this order, and may be related to the covering of the shell by the mantle. In *Kellia* and *Lasaea*, in which the shell is external, the foot can be withdrawn and the shell valves closed. In *Scintilla* the valves gape slightly (Deshayes, 1855), but less than in *Galeomma*, in which there is a permanent ventral gape, and in these species there is not only a gape, but the foot and part of the visceral mass extend permanently beyond the shell. In *Ephippodonta* the valves are semicircular, wide apart, and cannot be depressed to an angle of less than 70° . The animal is flat (Tate, 1887). The extreme case is found in *Libratula*, one of the Galeommatidae, in which the valves are normally perfectly horizontal and cannot be depressed to an angle of less than about 90° (Pease, 1855), but in this case the shell is external.

All members of the Lucinacea have an anterior inhalent opening and a posterior exhalent opening, and throughout the group the foot has a creeping sole.

In the species here examined for the first time there are two gill lamellae, two pallial openings, and the shell is completely enclosed in the mantle, which has papillae. There is a permanent gape between the shell valves, and the foot and part of the visceral mass extend permanently beyond the shell. The sexes are separate. It must therefore be included in the Galeommatidae and grouped with *Ephippodonta* and *Chlamydoconcha*, to which it is most closely related. In external appearance it most closely resembles *Chlamydoconcha*, but the shell is widely different (that of *Chlamydoconcha* being sword-shaped), the buccal hood is less prominent, the "anterior orifice" is absent, the papillae on the mantle are more numerous, the foot is longer and thinner, the adductor muscles are present, although reduced, and the habitat is different, the new species occurring in the burrows of *Lysiosquilla*, while *Chlamydoconcha* is found in stony clam-beds fixed to rocks or pebbles.

The animal differs from *Ephippodonta* in the form of the shell, that of *Ephippodonta* being semi-circular and covered in spines, with two bifid cardinal teeth in each valve. (These do not interlock.) The mantle lobes of *Ephippodonta* are free all round except dorsally, and the anterior margins of the mantle lobes are expanded and form a funnel. The foot is disc-shaped and very large, with a broad locomotory surface. There is also a difference in habitat. *Ephippodonta*, which was collected at Edithburg, Yorke Peninsula, South Australia (Tate, 1887), lives in the mud-formed burrows of a shrimp, sheltering beneath large stones between tide-marks.

The shell of the new species more closely resembles that of other members of the Galeommatidae, and is also similar to the shell of *Sciorberetia* (Bernard, 1895) and *Entovalva* (Anthony, 1916; Ohshima, 1930), both members of the Montacutidae.

It will be seen from the above that although this species must be included in the Galeommatidae, and is related to *Ephippodonta* and *Chlamydoconcha*, it differs to such an extent from both of these that it is reasonable to establish a new genus for its inclusion.

14. GENERIC AND SPECIFIC CHARACTERS.

Phlyctaenachlamys lysiosquillina gen. and sp. n.

HABITAT.—Occurs in the burrows of *Lysiosquilla maculata*.

Length of largest specimen in life : 2.4 cm.

Particulars of Type Specimen in the British Museum (N. H.): Length 6.0 mm. Shell, 4.75 × 3.0 mm. Mantle covered with papillae; these are not sensory, but have many mucous glands. Two large retractile tentacles at the anterior end; these are enlarged papillae. Mantle forms a hood over the anterior portion of the foot. Well-developed muscle layer in the mantle. Exhalent opening situated on a round protuberance posteriorly. Shell completely enclosed in the mantle; reduced, smooth, white and fragile, oval in shape and inequilateral. Gape between the shell valves ventrally; the mantle, foot, visceral mass and ctenidia extend permanently beyond them. Hinge teeth reduced. Internal elastic ligament. Adductor muscles reduced. Foot in two parts; anterior portion wedge-shaped; posterior portion long and thin. Foot contains many mucous glands, as well as a byssal gland. Ctenidia have no interlamellar junctions. Style-sac separate from the intestine. Intestine has no typhlosole. Rectum has no mucous glands. Sexes separate.

15. DISCUSSION.

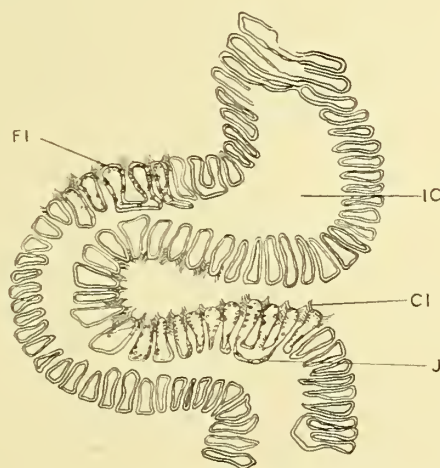
Phlyctaenachlamys lysiosquillina is a commensal from the burrows of *Lysiosquilla maculata*. The reduction of the shell, the covering of the shell by the mantle and the associated reduction of the hinge-teeth and the adductor muscles are adaptations in relation to this commensal mode of life.

In the Lucinacea an interesting series can be traced in the development of commensalism culminating in parasitism. *Kellia*, *Galeomma* and *Chlamydoconcha* are examples of the free-living members; *Ephippodonta* is commensal in the burrows of a prawn (Tate, 1887; Woodward, 1893); *Lepton squamosum* is commensal with *Upogebia stellata*; *Lepton clarkia* and *Mysella bidentata* with *Phascolosoma elongatum* (Salisbury, 1932); *Mysella bidentata* also with *Ophiocnida brachiata* (Winckworth, 1924) and *Montacuta ferruginosa* with *Echinocardium cordatum*. None of these is attached to the animal with which it is associated, and this is also the case in *Phlyctaenachlamys lysiosquillina*. *Montacuta substriata*, however, lives attached by byssus threads to the spines of *Spatangus purpureus* (Salisbury, 1932); *Entovalva semperi* lives attached to the body of a synaptid *Protankyra bidentata* (Ohshima, 1930); *Jousseáumia* in the basal chambers of the corals *Heteropsammia* and *Heterocyathus* (Bourne, 1906), while the extreme case is found in *Entovalva mirabilis*, which is an internal parasite in the gut of a holothurian (Voeltzkow, 1891).

Phlyctaenachlamys lysiosquillina produces byssus threads by which it may be attached to the sides of the burrow. The foot has a creeping sole, and movement is assisted by the unusual method of forcing water out from the mantle cavity by sudden violent contractions of the mantle. There are various modifications in relation to this form of movement, namely the development of an extensive layer of muscle in the mantle, and the

loss of the interlamellar junctions from the ctenidia. These interlamellar junctions are present in both *Chlamydoconcha* (Bernard, 1897) and *Ephippodonta* (Ridewood, 1903) and throughout the group, although Bernard records similar, although presumably less extensive, movements in *Chlamydoconcha*. This form of ctenidium will offer less resistance to the stream of water than one with a greater rigidity, and will be better able to withstand the considerable strain put upon it, due to the increase of pressure in the infrabranhial cavity when the mantle contracts.

The absence of mucous glands in the rectum is probably also associated with this movement of water through the mantle cavity. Particles of faecal matter will be shot out through the exhalent opening. There is thus no necessity for the formation of firm faecal pellets, because, owing to the violent expulsion of water, there will be less danger of the mantle cavity silting up.



TEXT-FIG. 21.—Ctenidium. $\times 150$. CI, cilia; FI, filament; IC, interlamellar cavity; J, interfilamentary junction.

The presence of a direct food current in an anterior to posterior direction, which represents the movement of the inhalent aperture from its primitive position, ventral to the exhalent aperture at the posterior end, to the anterior end, occurs only in the Order Lucinacea. It is clearly correlated with the absence of the burrowing habit in these animals, and probably with their mode of progression by means of a creeping sole. It is certainly mechanically efficient, as the ctenidia will act as “strainers” in the line of a direct current of water passing through the mantle cavity.

16. REFERENCES.

- ANTHONY, R. 1916. Contribution a l'étude de l'*Entovalva (Synapticola) perrieri*, Malard. Mollusque acephale commensal des Synaptés. Arch. Zool. Expér. Gén. LV, pp. 375-391.
- BERNARD, F. 1895. *Sciorberetia australis* type nouveau de Lamellibranche. Bull. Sci. France Belg. XXVII, pp. 364-395.
- 1897. *Chlamydoconcha orcutti*. Ann. Sci. Nat., Zool. (8) III, pp. 220-250.
- BOURNE, G. C. 1906. On *Jousseaumia*. Cey. Pearl Oyster Fish. Rep., Roy. Soc. London, V, pp. 243-266.
- DALL, W. H. 1884. *Chlamydoconcha*. Science, IV, pp. 50-51.
- DESHAYES, G. P. 1855. Sur le genre *Scintilla*. Proc. Zool. Soc. London, 1855, p. 171.
- FISCHER, P. 1887. Sur un nouveau type de Mollusque. *Chlamydoconcha*. Man. de Conchyl. et de Palaeont. Conchyl., 1887, pp. 201-206.

- OHSHIMA, H. 1930. Preliminary Note on *Entovalva semperi* sp. nov., a Commensal Bivalve Living Attached to the Body of a Synaptid. Annot. Zool. Jap. XIII, pp. 25-26.
- PEASE, W. 1865. Descriptions of New Genera and Species of Marine Shells from the Islands of the Central Pacific. Proc. Zool. Soc. London, 1865, pp. 512-517.
- PELSENEER, P. 1911. Les Lamellibranches de l'Expédition du Siboga. Partie Anatomique. Siboga-Expédition. Mon. LIIIa.
- RIDEWOOD, W. G. 1903. On the Structure of the Gills of the Lamellibranchia. Phil. Trans. Roy. Soc., B, CXCIV, pp. 147-284.
- SALISBURY, A. E. 1932. On *Lepton squamosum* and *Montacuta ferruginosa* and some other molluscs observed at the Salcombe Estuary, Devon. Proc. Malac. Soc. London, XX, pp. 100-103.
- TATE, R. 1887. Descriptions of some New Species of Marine Mollusca from South Australia and Victoria. Trans. Proc. Rep. Roy. Soc. S. Aust. XI, pp. 62-75.
- VOELTZKOW, A. 1891. *Entovalva mirabilis* eine schmarotzende Muschel aus den Darm einer Holothurie. Zool. Jahrb. Abt. Syst. V, pp. 619-628.
- WINCKWORTH, R. 1924. Specimens of Molluscs and Other Animals associated with them Found in a Day's Digging at Salcombe. Proc. Malac. Soc. London, XVI, p. 1.
- WOODWARD, M. F. 1893. *Ephippodonta MacDougalli*. Proc. Malac. Soc. London, I, pp. 20-25.
- YONGE, C. M. (1936) The Evolution of the Swimming Habit in the Lamellibranchia. Mém. Mus. Roy. d'Hist. Nat. Belg. (2), Fasc. 3, pp. 77-100.

19 APR 1940
PRESENTED

